TORREYA

Vol. 32 July-August, 1932 No. 4

Observations on the flower behavior of the Avocado in Panama

Alexander F. Skutch

About the pleasant grounds of the Research House of the United Fruit Company fronting on the Changuinola Lagoon twenty miles west of Almirante in western Panama, where I resided during the first half of the year 1929, stood about a dozen well-grown avocado trees (*Persea americana* Mill.), some of them very large, well-rounded specimens. While the history of these particular trees is not definitely known, and they were undoubtedly planted at widely separated intervals, they all probably represented the usual unpedigreed and ungrafted stock, such as one finds in the dooryard plantings of the natives throughout the region. The heavy solstitial rains abated early in January, and gave way to the delightful weather which prevails in the region during the early months of the year. The days were generally clear, although the sky was sometimes overcast it seldom rained, and at noon the temperature in the shade rarely exceeded 80° F. In such weather, about the middle of January, the earliest avocado trees began to flower, and thence until the middle of March some of the trees were in blossom. At the same time they shed the old leaves of the previous season, and acquired a new covering of bright green.

Having read a paper by Robinson and Savage (1) on the pollination of the avocado in Florida, I was eager to observe for myself the interesting and peculiar floral behavior which they recorded. A friend familiar with tropical fruit trees with whom I discussed the matter seemed to doubt whether the avocado—at least in the tropics—actually exhibited the double period of anthesis which these authors describe, which made me the more interested to determine for myself what the situation actually was. Although we have several excellent accounts of the anthesis of improved and grafted avocados in subtropical California and Florida, I am not aware that anything has been published, at least in the American botanical

literature, concerning the behavior of the flowers of unimproved trees in the tropics. Since such trees seem closer to the ancestral wild stock than the highly selected varieties chosen by commercial orchardists, a record of the behavior of a few of them might contain certain points of interest.

Stout's careful studies of the flower behavior and the pollination of the avocado (2, 3), begun in southern California during the winter of 1922-23, are the basis of our knowledge of the subject. He discovered that each flower has two distinct periods of opening, separated by a period of variable duration in which it is closed. During the first opening the anthers remain closed and shed no pollen, but the pistil is receptive to pollen brought from other trees. In the intervening closed period the stigma withers, with the result that at the second opening of the flower on the following day, when the anthers dehisce and shed their pollen, self-pollination is no longer possible. Since all flowers of a set on the same tree behave in the same manner, opening and closing simultaneously, agreeing in the condition of their anthers and stigmas, with slight or no overlapping of the first and second opening of different flowers, close-pollination is very unlikely to occur.

In respect to their periods of dianthesis, all avocados so far studied fall into two distinct groups. In the one, which Stout has designated as Class A, the flowers open first with receptive stigmas in the morning, when we may for conciseness term them "functionally pistillate," close some time during the middle of the day, remain closed for about twenty-four hours, and open the second time to shed their pollen during the afternoon of the succeeding day. After persisting a few hours as functionally staminate flowers, they close in the late afternoon and never again expand. Trees of Class B are characterized by the fact that their flowers open first in the afternoon,—like the former functionally pistillate during the first anthesis,—and close again late in the day, but on the basis of the time of the second expansion their flowers fall into three groups. In the first (B_1), all the flowers of the tree open for the second time and shed their pollen over a period of several hours the following morning. The life of these flowers is roughly 24 hours. In the second (B_2), after closing at the end of their first period of expansion, the flowers remain closed during two nights and a day, and open again only on the second morning following, when they shed their pollen as in the case of the preceding group. Their life

Fig. 1. The inflorescence of the avocado. The flowers are borne on the basal branches of the newly expanding annual growth increment of the shoot, the terminal portion of which bears the young leaves of the season. February 12, 1929.

is then about 48 hours. The third group (B_3) is made up of trees that bear some flowers which exhibit the behavior of each of the preceding groups. That is, after the termination of their first period of anthesis, some will remain closed a single night and open the following morning, while others on the same tree will remain

Fig. 2. The reciprocal alternations of the development of the pistils and anthers of avocado flowers. At right, flowers of Taylor, a typical Class A variety; at left, flowers of Panchoy, typical of Class B. The upper photograph shows the appearance of the two classes at the same moment in the forenoon, the lower in the afternoon, when a different set of flowers is open on each tree. In the morning, Class A flowers in their first opening (upper right) are receptive to the pollen which is shed by Class B flowers in their second opening (upper left). In the afternoon, Class A flowers in their second opening (lower right) shed pollen which may be carried to the receptive stigmas of Class B flowers in their first opening (lower left). Photograph by Dr. A. B. Stout.

closed two nights and a day, and expand again on the second morning following.

During the morning, bees and other insects may carry pollen from Class B trees with flowers in their second opening to the receptive stigmas of Class A flowers in their first opening, while during the afternoon the process is reversed.

All trees of the same horticultural variety belong to the same class and their flowers open and close, under like weather conditions, at about the same time. Indeed, since they are all derived by vegetative means of propagation from the same tree, they behave exactly as though they were branches of a single individual.

Stout in California and Florida and Robinson and Savage in Florida have determined the classification of a large number of named varieties.

The small, yellowish flowers of the avocado are borne in panicled clusters on short, leafless branches at the base of the annual shoot (Fig. 1). The fully expanded blossom measures about 12 mm. in diameter. The six perianth divisions are alike in size and color. There are nine stamens arranged in two rows, the six of the outer series situated opposite the perianth divisions, the three of the inner series inserted just inside of those three of the outer series which lie opposite the outer perianth divisions or sepals. In the center of the flower is a single one-ovuled pistil with short style and simple, capitate stigma. During the first opening, when the stigma is receptive, the nine stamens with their closed anthers are bent outward and lie above the inner face of the perianth divisions, leaving the stigma fully exposed (2, Fig. 2). At the second opening, when the stigma is usually discolored, the three inner stamens, their filaments somewhat elongated, stand upright in the center of the flower overshadowing the pistil, while the other six curve obliquely upward (4, Fig. 2). Each anther opens by four neat, uplifted, elliptical valves and sheds its yellowish pollen.

After I had become familiar with the general type of behavior of the trees by preliminary observations, I devoted February 16 and 17, 1929, both clear, warm days, to the observation of eight trees whose lower branches were accessible from the ground or from an eight-foot step-ladder. On each of six of these trees twenty flowers were marked with small jeweller's tags, so there could be no doubt of the behavior of individual blossoms. Both days, from 7:30 A.M., when the earliest flowers were opening, until sun-

set, when the last flowers closed, were spent in a continuous round from tree to tree. Less continuous observations to determine certain points of interest were made on subsequent days. The eight trees fell into three well-marked groups.

I. Two trees growing side by side agreed essentially in their floral behavior. Both belonged to class A. The fresh flower buds began to open in the morning at 9:20, and by 9:30 some were completely expanded. The stigmas were fresh and apparently receptive, the filaments declined and the anthers closed. Thus they remained during the remainder of the morning. By 12 noon some flowers began to close; by 12:30 many were closed and others still closing. The flowers then remained closed for slightly more than 24 hours, or until about 1 P.M. the following day, when they began to expand for the second time. The stigmas of most had withered but in a few cases they still appeared fresh. The anthers began to shed their pollen about 15 minutes after the flowers opened. At 4:40 P.M. the flowers began to close, at 5 they were about one-half closed, and at 5:20 completely closed.

These trees, especially the smaller, set a fair quantity of fruit.

II. Two large trees belonged to class B. In both the flowers opened for the first time between 2:30 and 3:20 P.M. and remained in anthesis with receptive stigmas during the latter part of the afternoon, different individuals closing for the night between 4:45 and 6 P.M. They opened the following morning, some with stigmas still fresh in appearance, between 7:30 and 8, and having shed their pollen, made their final closing between 1:10 and 2:30 P.M.

One of these trees, when I left Almirante in June gave promise of a fair crop, while the second bore only a few green fruits.

III. Four of the trees, while giving indications of floral behavior which would place them in class B, were extremely erratic in their anthesis. A small percentage of the flowers opened sporadically during the late afternoon, between 3:30 and 4 on different trees, and remained open for less than two hours, for by 5:30 or 5:45 all were again tightly closed. The degree of spreading of the perianth of these flowers was variable; many opened only very slightly, few of them spread fully in the normal manner. The following morning, between 7:30 and 8, all of those flowers which showed any degree of opening on the previous afternoon, together with many which now for the first time expanded, opened with stigmas still fresh, and soon the valves of the anthers lifted and allowed the pollen to escape. These flowers now remained open for

a long period, about six hours, and did not close until between 1 and 2 P.M., when many of the stigmas were still unwithered.

I made observations to determine what proportion of the flowers opened partially or completely on the afternoon before expanding for what would normally have been their second period of anthesis on the following morning. At 4:20 P.M., February 18, the middle of the desultory first period of anthesis, I marked a twig on tree 2 which bore ample clusters of buds but only a single open blossom. On the following morning over 100 flowers on this twig were open and shedding pollen. Other twigs on this tree and its neighbor tree 3 showed a similar low proportion of the flowers with two periods of anthesis. The other two trees in this group had a larger proportion of flowers which opened in the afternoon, but still well under 50 per cent, of the total number. Thus on February 18, at 4:10 P.M., 25 flowers on a marked twig of tree 4 were more or less open. The following morning at 10:40 this twig supported 69 blossoms in full anthesis.

It occurred to me later that all, or at least a much greater proportion of the flowers than the observations just recorded would indicate, might have a very transitory afternoon opening. If such were the case, and the flowers did not all open at the same time, a single examination even in the middle of the first period of anthesis would not reveal their true numbers. Accordingly, on February 25, certain chosen branches on these trees were visited at twenty-minute intervals, and every flower which showed any degree of opening was tagged. A single example will suffice. At 1:10 P.M. the chosen branch on tree 1 bore 107 open flowers in their second period. Since the sky was overcast most of the day, the closing of these flowers was delayed; it began at about two and was not completed until three o'clock. By 4:15 P.M. a few first period flowers had opened on other accessible branches of the same tree, but none on the selected branch. Between 4:55 and 5:15 one flower on this branch opened halfway. It never expanded beyond this point and by 6:25 was practically closed again. Yet next morning this same branch bore 49 open flowers, including that which had partly opened on the preceding afternoon. Similar observations on trees 3 and 4 gave comparable results. On the succeeding afternoon, which was bright and warmer, a larger number of flowers opened on these trees, but still a small percentage of those which expanded the ensuing morning.

Although in a large proportion of the flowers of these four

trees the stigmas remained apparently receptive during the second period opening, so that there was a good possibility of the transfer to them of pollen from the same flower and of other flowers of the same or the three neighboring trees in class B, the irregular character of the first opening made the accomplishment of what we may term the "legitimate pollination" of these flowers by the two neighboring class A trees extremely unlikely. When I examined these four trees at the end of March I could find only a single immature fruit in the whole group, despite the myriad blossoms each tree had expanded.

Stout and Savage and Robinson have demonstrated that abnormal weather, especially a cold spell, may cause great disturbances in the daily periodicity of the flowers, amounting sometimes to the complete inhibition of the first period opening. The result is a set of flowers which exhibit only a single period of anthesis, when the pollen is shed. The peculiar behavior of the four trees in my third group was certainly not conditioned by atmospheric conditions, for it occured during warm, bright weather as well as on cloudy and rainy days, and was the usual behavior of the trees in question. It may be noticed in passing that the two trees of group II show an approach to the condition of group III in their relatively brief first period opening (less than 3 hours) followed by a second period of anthesis over twice as long on the following day.

It is hardly an exaggeration to state that a large avocado tree produces millions of flowers each season, and only an exceedingly small proportion of these set fruit even under the most favorable conditions. The normal fate of the flower is then to fall shortly after closing for the second time—by the second day after this final closing most have been shed, by the third day practically all save the few which set fruit. During the height of the flowering season there is a constant shower of effete blossoms, and the ground beneath the trees is thickly strewn with them. The continuous dropping of the closed blossoms reminds one of the sifting down of the corollas of grape flowers beneath a wild vine which is coming into full bloom. As a breeze shakes the bare limbs, the pattering of falling flowers upon the dry leaves which cover the ground beneath the tree sounds like the rustling of the first flakes of an early snow upon the dead leaves of an autumnal forest in the north. After the flowers fall, the naked branches of the inflorescence are themselves

cut off from the tree, and finally in many cases the entire inflorescence—when it does not support developing fruit.

As the earliest flower buds expanded in the latter half of January, the trees began to cast off the old foliage which had served them ten or eleven months. As is frequently the case with deciduous tropical trees whose flowers are produced when the limbs are almost or quite leafless, both the process of defoliation and the expansion of the flowers begin and progress most rapidly at the top of the tree, with the result that this usually becomes quite bare of foliage while the lower branches are still well-clothed with the old leaves (see Wright 4, p. 475). Not only are the lower branches the last to lose their old leaves, but they are the first to acquire the new, which are in many cases put forth and sometimes even attain full size before the old leaves in the same part of the tree have been completely shed. Thus it happens that the lower stories of some trees are never bare, while the upper half is often denuded of foliage during at least a considerable part of the period of flowering. Frequently, however, a tree will be found quite leafless at the height of the flowering season, when it is yellow with the myriad buds and blossoms it supports. As with the sassafras, the flowers themselves are borne on leafless branches which spring from the base of the newly expanding annual shoot, and consequently are situated below the young foliage. The tender leaves are a very light green and contrast strongly with the sombre hue of the old foliage still persisting on the tree. By the second week of March, 1929, some of the trees had completed their flowering, while in others flowers were still produced on the upper branches, after the lower had spent all their buds. About half the trees were in full new foliage, but a few were still rather bare.

Summary

Observations were made on the flower behavior of eight avocado trees in a dooryard planting in western Panama. Two of these were typical class A trees, as defined by Stout, and two belonged to class B_1. The other four, while giving indications of the type of behavior of class B trees, were erratic in that only a small percentage of the flowers opened in the afternoon. In most the first period opening was suppressed entirely, and there was a single long period of anthesis in the morning, when the pollen was shed at the same time the stigmas of the same flowers appeared recep-

tive. The four trees of normal behavior set a fair crop of fruit, while only a single fruit was produced by the latter four.

Literature cited

1. Robinson, T. Ralph and Savage, E. M. Pollination of the avocado. U. S. Dept. Agric. Circular 387, p. 1-16. 1926.

2. Stout, A. B. A study of cross-pollination of avocados in southern California. Ann. Rept. California Avocado Assoc. 1922-1923: 29-45. 1923.

3. ———. The flower behavior of avocados. Mem. New York Bot. Gard. 7: 145-203. 1927.

4. Wright, H. Foliar periodicity of endemic and indigenous trees in Ceylon. Ann. Roy. Bot. Gard. Perideniya 2: 415-516. 1905.

Baltimore, Maryland